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The Mast Cells

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ABSTRACT

Mast cell is one of the important cells in the immune system. It is derived from multipotent hematopoietic progenitor cells. The mast cell produces a number of cytokines to augment immune responses, growth, and differentiation of other cells. This cell also exhibits multifunctional roles in health and diseases. This review provides board overview of the mast cell including mast cell discovery and development, characteristics of mast cells, mast cell activation, regulation and functions in health and diseases. Understanding hallmark of the mast cell will benefit the development of therapeutic approaches of the mast cell in the future.

Abbreviations: CTMCs: Connective Tissue Mast Cells; MMCs: Mucosal Mast Cells; SCF: Stem Cell Factor; SYK: Spleen- Associated Tyrosine Kinase; BTK: Bruton's Tyrosine Kinase

The Mast Cell

Mast cells are bone marrow derived hemopoietic cells (Kitamura, et al. [1-3]). The mast cell is one of the important cells in the immune system. It is derived from multipotent hematopoietic progenitor cells. The mast cell produces a number of cytokines to augment immune responses, growth, and differentiation of other cells. This cell also exhibits multifunctional roles in innate immunity against bacterial and parasite infections, immediate and delay hypersensitivity reactions, inflammation, fibrosis, autoimmune pathology neoplasia, wound healing and angiogenesis (Mekori, et al. [4-9]). Unlike the other hematopoietic cells, mature mast cells maintain their ability to proliferate under normal conditions (Metcalfe, et al. [7]). Mast cell progenitors express many transcription factors and need GATA-2, PU.1 transcription factors for their survival and development (Tsai, et al. [10,11]).

Mast Cell Discovery and Development

The mast cell was first identified as a cell containing metachromatic properties in connective tissue by Paul Ehrlich who believed that overfeeding of this cell generated inclusion bodies inside the cell (Ehrlich, et al. [12,13]). Rodent mast cells can be categorized into two classes, connective tissue mast cells (CTMCs) and mucosal mast cells (MMCs), based on their histochemical heterogeneity (Enerback, et al. [14-16]). Mucosal mast cells stained with Alcian blue because of the predominant chondroitin sulfate proteoglycan in the granule contents. On the other hand, connective tissue mast cells containing heparin as a major proteoglycan in the granule stained with Safanin but not Alcian blue. CTMCs are distributed in the entire connective tissues of skin, in the peritoneal cavity, adjacent to blood vessels and to peritoneal nerves, whereas MMCs are present in the lung and the intestinal lamina propia (Aldenborg, et al. [17,18]). These two subtypes of mast cells have some different functions, e.g. MMC proliferate profoundly during T-cell dependent immune responses to certain intestinal parasites (Schmitt, et al. [19,20]), while CTMC exhibit a normal proliferation profile (Aldenborg, et al. [17]). In humans, there are three subsets of mast cells that have been characterized:

1. MCT, which expresses tryptase and resides primarily in the alveolar septa of the lung and in the small intestinal mucosa;
2. MCTC, which expresses tryptase, chymase, carboxypeptidase A (CPA) and cathepsin G and resides primarily in the skin and in the small intestinal submucosa;
3. MCc, which expresses chymase but lacks tryptase (Schwartz, et al. [21-26] Dahlin et al., 2020).

Based on tissue location, the human MCT is related to the rodent MMC and the MCTC is related to the rodent CTMC. In the murine system, stem cell factor (SCF) and IL-3 are essential for mast cell maturation while human mast cells need only SCF but not IL-3 for their development (Huang, et al. [27-33]). The recently described MCc subset can also be differentiated from normal human hematopoietic stem cells in vitro (Li, et al. [24]) Murine bone marrow cultured in SCF and IL-3 gives rise to populations of mast cells that most resemble the connective tissue phenotype (Tsai, et al. [31]). CD34+ stem cells from human cord blood, peripheral blood (Rottem, et al. [34,35]) and fetal liver (Irani, et al. [36]) in the presence of SCF will differentiate into human mast cells. In addition to IL-3 and SCF, the proliferation and differentiation of mast cells can be enhanced by adding other growth factor including IL-4, IL-9, IL-10 and nerve growth factor (Hultner, et al. [37-39]). The mast cell progenitor first appears in the yolk sac at day 10 of gestation. Unlike mast cell precursors in fetal liver and bone marrow, mast cell progenitors in yolk sac are uni-potential for mast cells in the presence of SCF and IL-3. Mast cell precursors express the high affinity IgE receptor (FcεRI) and FcγRII/III before granulation (Rottem, et al. [40-44]). Mast cells are believed to leave the bone marrow as non-granulated mast cells and complete their differentiation as mature mast cells in mucosal and connective tissue where they differentiate into tissue- specific mast cells (Dahlin, et al. 2020).

Characteristics of Mast Cells

Mature mast cells express a diverse array of cell surface antigens. The most important are c-Kit (a receptor for SCF which promotes mast cell maturation, survival and adhesion) and the FcεRI which plays a crucial role in IgE-mediated allergy and also in mast cell maturation (Cop, et al. [45-47]). It has been reported that bone marrow cultured in the presence of IL-3 exhibits the mRNA expession of the three subunits α, β and γ of FcεRI in a week and this expression continues to increase over 3 weeks during mast cell development (Rottem, et al. [40,41]). These studies also show that the cells containing low FcεRI often contain few granules and thus lack the morphologic characteristics of mature mast cells. In addition, the FcεRI positive cells have proliferative potential but are slower than the mast cell progenitors that do not yet express FcεRI. These findings suggest that FcεRI expression on mast cells is a marker of terminal differentiation, and this receptor expression may also provide cells to respond to the growth factors and other stimuli before they exhibit granule maturation and are morphologically recognized as mature mast cells (Rottem, et al. [40]). Mature differentiated mast cells maintain their CFU-mast characteristic feature (Metcalfe, et al. [7]) which is capable of continuing proliferation under normal conditions. This unique characteristic of mast cells distinguishes them from other hematopoietic cells, e.g. basophils, neutrophils and eosinophils. Adhesion of mast cells to extracellular matrix compartments is mediated by many adhesion molecule receptors expressed on the cell surface of mast cells such as laminin, fibronectin, VLA-3, VLA-4 and VLA-5, vitronectin receptors (Columbo, et al. [48-50]). Cross-linking of FcεRI on BMMC has been reported to promote the attachment, and this adherence occurred at a lower dose of antigen challenge than that required for histamine release (Thompson, et al. [51]). Culture of mast cells with TGF-β enhances IgE-mediated adhesion of mast cells to laminin (Mecalfe, et al. [7]), and SCF also promotes the adhesion of IL-3-dependent BMMC to fibronectin in a dose dependent manner (Dastych, et al. [52]). However, IL-1, IL-2, IL-3, IL-4, IFN-γ, TNF and GM-CSF have no activation effect on the adhesion of mast cell to laminin (Thompson, et al. [51]). Mast cells also have been found to interact with lymphocytes in inflamed tissue, during bacterial and parasitic infections (Friedman, et al. [47,53-55]).

Mast Cell Activations

Mast cell activation can be achieved via FcεRI dependent and FcεRI independent pathways (Cop, et al. [45,47]). The activation of mast cell through FcεRI dependent pathway is started by cross linking of FcεRI receptors after interaction with IgE bound antigen. Many compound and cytokines are also known as mast cell activators by FcεRI independent pathway such as compound 48/80 (Ortner, et al. [56]), mastoparan, polymyxin B and other basic amino acid polymers (Lagunoff, et al. [57]), Rab3A (Oberhauser, et al. [58]), IL-1, IL-3, and GM-CSF platelet factor 4 and SCF (Alam, et al. [59-63]), C3a, C4a, C5a (Demopoulos, et al. [64,65]), dextrans and lectins (Lagunoff et al. [57]). After activation mast cells release mediators form granules (histamin, mast cell proteinase MMCP1-5, tryptase MMCP6-7, carboxypeptidase A or CPA). Activated mast cells also synthesize and release new mediators from cyclooxygenase products (prostaglandins and thromboxanes) and lipoxygenases (leukotrienes, LTs). In addition, mast cells generate a variety of cytokines such as TNF-α, IFN-γ, GM-CSF, MIP-1β, T-cell activation gene (TCA)-3, IL-2, IL-3, IL- 4, IL-5, Il-6, IL-10, IL-12, IL-13 (Burd, et al. [54,66-70] Dahlin et al. 2021, Levi-Schaffer, et al. [47,71])

Mast cell Regulations

The rate of cell proliferation and cell death, which is often due to apoptosis, are the key regulators in cell homeostasis (Arends, et al. [72]). In mast cells, IL-3 is important for early mast cell proliferation and SCF is important for mast cell differentiation. SCF also promotes mast cell adhesion to the extracellular matrix (Tsai, et al. [31,52,73]). Mast cells undergo apoptosis after removing IL-3. However, SCF (but not insulin growth factor and NGF) can prevent apoptosis in both in vitro and in vivo systems (Mekori, et al. [74,75]). Many therapeutic approaches were developed to inhibit mast cell activation via blocking IgE receptor (FcεRI) activation and inhibit signaling transduction pathway involving mast cell degranulation and mediator release e.g.

Bruton's tyrosine kinase (BTK) and spleen- associated tyrosine kinase (SYK). Inhibitors of BTK or SYK down regulate the degranulation of human mast cells induced via FcεRI (Dahlin et al. 2021).

Mast Cell Functions in Health and Diseases

Mast cells perform multiple biological functions such as innate immunity against bacterial and parasite infections, immediate and delayed hypersensitivity reactions, inflammation, fibrosis, autoimmune pathology neoplasia, wound healing, angiogenesis (Mekori, et al. [4-7]). Mast cells can produce and respond to physiological mediators and chemokines to modulate inflammation. As long-lived, tissue-resident cells, mast cells indeed mediate acute inflammatory responses such as those evident in allergic reactions. In addition, mast cells participate in innate and adaptive immune responses to bacteria, viruses, fungi, and parasites. Moreover, mast cells release several cytokines to recruit other immune effector cells to the infection area which induced many inflammatory disorders of host tissues. Mast cell also exhibit pathological roles in autoimmune diseases including rheumatoid arthritis and chemokines including CXCL12, CCL2, CCL3, CCL4, and CCL5 leading to tissue destruction (De Filippo, et al. [76-78]). The control of mast cell activation or stabilization is a powerful tool in regulating tissue homeostasis and pathogen clearance. Moreover, mast cells contribute to maintaining the homeostatic equilibrium between host and resident microbiota, and they engage in crosstalk between the resident and recruited hematopoietic cells (Anna Sobiepanek, et al. 2022) (Krystel-Whittemore M, et al. [79]).

Conclusion

Mast cell exerts many biological roles in both innate and adaptive immune responses which affect human health and diseases. Understanding hallmark of the mast cell development, characteristics, activation, regulation and functions in health and diseases can benefit the development of therapeutic approaches of the mast cell in the future.

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